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Deciphering the early evolution of echinoderms with Cambrian fossils

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Abstract: Echinoderms are a major group of invertebrate deuterostomes that have been an important component of marine ecosystems throughout the Phanerozoic. Their fossil record extends back to the Cambrian, when several disparate groups appear in different palaeocontinents at about the same time. Many of these early forms exhibit character combinations that differ radically from extant taxa, and thus their morphology and phylogeny have long been controversial. Deciphering the earliest evolution of echinoderms therefore requires a detailed understanding of the morphology of Cambrian fossils, as well as the selection of an appropriate root and the identification of homologies for use in phylogenetic

analysis. Based on the sister-group relationships and ontogeny of modern species and new fossil discoveries, we now know that the first echinoderms were bilaterally symmetrical, represented in the fossil record by *Ctenoimbricata* and some early ctenocystoids. The first radial echinoderms are the helicoplacoids, which possess a triradial body plan with three ambulacra radiating from a lateral mouth. Helicocystoids represent the first pentaradial echinoderms, and have the mouth facing upwards with five radiating recumbent ambulacra. Pentaradial echinoderms diversified rapidly from the beginning of their history, and the most significant differences between groups are recorded in the construction of the oral area and ambulacra, as well as the nature of their feeding appendages. Taken together, this provides a clear narrative of the early evolution of the echinoderm body plan.

Key words: Deuterostomia, Echinodermata, morphology, phylogeny, rooting, homology.

ECHINODERMS are one of the most successful groups of marine invertebrates ever, with around 10,000 extant species belonging to five classes (asteroids, crinoids, echinoids, holothurians and ophiuroids), as well as a rich fossil history consisting of about 30 extinct Palaeozoic clades (Sumrall and Wray 2007) and dating back to the Cambrian (Zamora *et al.* 2013a). They are unique among bilaterians in exhibiting pentaradial symmetry as adults, having departed radically from the bilateral ancestral body plan (Smith 2008). Echinoderms are also characterized by a plated calcite skeleton with a mesh-like microstructure called stereom (Bottjer *et al.* 2006) and a water vascular system: a network of fluid-filled canals and tube feet (arranged into zones called ambulacra) used in feeding, locomotion, respiration and waste transportation (Nichols 1972). These characters can be easily identified in extant groups, but are absent or highly modified in some of the earliest fossil forms. As a result, the

phylogenetic relationships of early echinoderms are extremely controversial (David *et al.* 2000; Smith 2005), hindering efforts to decipher the evolutionary emergence of the phylum.

Molecular phylogenies provide a robust framework for understanding how major groups of animals are related, and consistently recover a sister-group relationship between echinoderms and hemichordates (Bourlat *et al.* 2006; Dunn *et al.* 2008; Philippe *et al.* 2011), with crinoids the sister group of all other extant echinoderms (Mallatt and Winchell 2007; Janies *et al.* 2011; Telford *et al.* 2014). However, such analyses cannot elucidate the earliest evolution of echinoderms because the majority of clades are extinct; the five extant classes first appear in the Lower to Middle Ordovician, but the phylum traces its roots back to at least Cambrian Stage 3 (~ 521 Ma), when the earliest fossil echinoderms appear at approximately the same time in Gondwana and Laurentia (Zamora *et al.* 2013a). The origin of echinoderms was most probably earlier still, with recent molecular clock analyses placing the divergence between echinoderms and hemichordates in the Ediacaran, about 580–550 Ma (Peterson *et al.* 2008; Erwin *et al.* 2011). The stereom skeleton presumably originated slightly later, just prior to the first appearance of echinoderms in the fossil record, and might have coincided with the transition from an aragonite sea to a calcite sea that occurred in the upper part of Cambrian Stage 2 (Kouchinsky *et al.* 2012; Smith *et al.* 2013). A recent survey of the Cambrian record of echinoderms identified 188 species belonging to eight major groups (Zamora *et al.* 2013a). Study of these fossils should shed light on the first steps in the evolution of the echinoderm body plan.

Our understanding of the morphology of Cambrian echinoderms has improved considerably in recent years, informed by the discovery of important new fossils and the application of powerful imaging techniques (Rahman and Clausen 2009; Zhao *et al.* 2010; Zamora and

Smith 2012; Zamora *et al.* 2012; Gorzelak and Zamora 2013; Smith and Zamora 2013). This has yielded valuable insights into the relationships and evolution of early echinoderms. Most significantly, we now have direct evidence from the fossil record of how the first pentaradial echinoderms emerged from their bilateral ancestors, enabling us to begin to unravel the sequence of character acquisition in the echinoderm stem group – even though a number of uncertainties still need to be addressed (Smith and Zamora 2013). The aim of this paper is to review the current state-of-the-art knowledge of Cambrian echinoderms, highlighting important recent findings that have helped us build up a more complete picture of the phylogeny and early evolution of echinoderms. We finish by outlining several outstanding questions, which will be a major focus of research efforts in the coming years.

WHAT MAKES AN ECHINODERM?

According to most classic zoology textbooks, the three main synapomorphies of echinoderms are a calcite endoskeleton with a mesh-like stereomic structure (Fig. 1F, G), pentaradial symmetry as an adult (Fig. 1A) and a water vascular system derived from the left coelom only. However, one or sometimes two of these traits are absent in several Cambrian groups; cinctans, ctenocystoids, solutes and stylophorans do not exhibit any trace of radial symmetry (Fig. 1B, C), and ctenocystoids (and possibly cinctans) lack an echinoderm-type ambulacral system (Smith 2005; Rahman and Clausen 2009; Zamora *et al.* 2012). In contrast, other Cambrian taxa, such as some edrioasteroids, clearly show "typical" echinoderm features, including pentaradial symmetry (e.g. *Kailidiscus*; Fig. 1H) and an ambulacral system with floor plates, cover plates and large basins for the tube feet (Fig. 1I–K) (Zhao *et al.* 2010). Cambrian echinoderms therefore represent a mosaic of different forms, with a mixture of ancestral and derived characters.

One feature that does seem to be common to all Cambrian echinoderms is the calcite endoskeleton. Although specimens with original calcite are rarely preserved, scanning electron microscope studies of isolated plates in which the skeleton has been secondarily replaced by other minerals (Clausen and Smith 2005, 2008; Clausen and Peel 2012) and cathodoluminescence analyses of fossils preserved as recrystallized calcite (Gorzelak and Zamora 2013) reveal stereom microfabrics in Cambrian forms that are similar to those observed in extant species (Fig. 1D, E). In modern echinoderms, stereom formation is governed by a suite of unique genes (Bottjer *et al.* 2006), and it seems likely that the same genes were responsible for biomineralization in the earliest fossil taxa (Gorzelak and Zamora 2013). Recent work has suggested that extant hemichordates also possess endoskeletal elements constructed from calcium carbonate and regulated by homologues of several of the genes that are responsible for stereom formation in echinoderms (Cameron and Bishop 2012); however, the putative hemichordate endoskeleton is made from aragonite rather than calcite, implying an independent origin of mineralized tissue in the two phyla. Thus, out of the three characters traditionally taken as echinoderm synapomorphies, only a stereom endoskeleton remains as a convincing derived trait shared by all echinoderms.

THE CAMBRIAN FOSSIL RECORD

Cambrian echinoderms exhibit a range of disparate morphologies, including bilateral, asymmetrical, spiral and pentaradial forms (Smith *et al.* 2013). All of these fossils are important as they document the early stages of echinoderm evolution; however, they can be difficult to interpret because they display unusual/unique character combinations that cannot easily be compared with one another, let alone with any extant taxa. Nevertheless, recent

developments in high-resolution, non-destructive imaging techniques (e.g. X-ray micro-tomography) have made it possible to elucidate previously enigmatic details in several Cambrian echinoderms. Furthermore, the discovery of new and exceptionally well-preserved fossils has shed light on the characters of a number of extinct forms. The exact number of Cambrian clades is unclear; Zamora *et al.* (2013a) recognized eight major groups, but this is clearly an underestimate of the total number of clades present in the Cambrian because several groups are almost certainly paraphyletic (e.g. edrioasteroids and eocrinoids). In the following section, we briefly describe the main characteristics of those forms that are most critical to deciphering the Cambrian evolution of echinoderms.

Ctenoimbricata has a bilaterally symmetrical theca and lacks any appendages (Sup. data 1). The theca is bordered by a ring of marginal plates, and is covered dorsally by a partially calcified membrane with embedded spiny ossicles and ventrally by a membrane of tessellate plates. *Ctenoimbricata* possesses a very wide anterior orifice, which has been interpreted as an inhalant and exhalant opening; the position of the anus is unclear, but it is inferred to have opened at the posterior (Zamora *et al.* 2012). The anterior opening is dorsally protected by a flat roof of imbricate plates and a large central suroral plate, while its ventral part is bounded by a number of knife-like ossicles (Zamora *et al.* 2012).

Ctenocystoids have a bilateral to weakly asymmetrical theca without a stem or typical ambulacra (Figs. 1B, 2F–H). The theca is framed by one or (more frequently) two superposed rings of large marginal plates; the dorsal and ventral surfaces of the theca are covered by tessellated membranes of small polygonal plates. At the anterior of the theca, a specialized organ composed of a series of tooth-like plates and a large suroral plate, called the ctenidium or ctenoid apparatus, encloses a pair of narrow grooves. This structure covers the mouth and

presumably controlled feeding, although the exact mechanism is debated (Parsley 1999; David *et al.* 2000; Rahman and Clausen 2009). A single cone-shaped aperture is located at the posterior of the theca and is universally agreed to mark the position of the anus (Robison and Sprinkle 1969; David *et al.* 2000; Domínguez Alonso 2004; Rahman and Clausen 2009).

Cinctans have an asymmetrical theca with a posterior appendage (stele) (Fig. 2A–C). The theca consists of a single ring of robust marginal plates, termed the cinctus, which surrounds dorsal and ventral membranes of tessellated plates. Three major openings are located at the anterior of the theca. The mouth is a circular opening in the anterior right of the cinctus. The porta is a large opening that penetrates the cinctus at the midline and is covered by a large plate called the operculum; the function of this orifice is debated, and it is interpreted as an exhalant opening for either anal (e.g. David *et al.* 2000) or atrial (e.g. Smith 2005) outflow. A pyramid of small plates pierces the dorsal surface of the theca and is taken as an anus (e.g. Smith 2005) or a gonopore (e.g. Parsley 1999). In addition, in some species small openings between plates (sutural pores) occur in the dorsal membrane (Friedrich 1993; Zamora & Smith 2008). One or an asymmetrical pair of food grooves, covered by multiple sets of small plates, run along the anterior margin of the cinctus into the mouth. At the posterior, the stele occurs as a rigid prolongation of the cinctus (Friedrich 1993; Jefferies *et al.* 1996; Zamora and Smith 2008; Rahman and Zamora 2009).

Solutes have an asymmetrical, polyplated theca with an appendage at either end (Figs. 1C, 2D). The short flexible appendage at the anterior is typically composed of two rows of floor plates that are opposed by two rows of smaller cover plates. The mouth is located at the base of this appendage, which is taken to be a feeding ambulacrum; it is debated whether this represents an arm (e.g. Smith 2005) or a brachiole (e.g. David *et al.* 2000), however because

there is apparently a direct connection between the interior of the theca and the appendage, it seems most probable that this is an arm. Hydropore and gonopore openings are situated near the base of the anterior appendage in many taxa. The longer appendage (stele) at the posterior is either made up of numerous unorganized platelets (i.e. *Coleicarpus*), or differentiated into a highly flexible proximal region and a rigid distal part (other solutes). The anus is a large opening surrounded by specialized plates, and is located close to the stele insertion (Jefferies 1990; David *et al.* 2000; Smith 2005; Noailles *et al.* 2014).

Stylophorans have an asymmetrical theca and a single appendage (Fig. 2E). The class is usually divided into two orders: cornutes and mitrates. In cornute stylophorans, the theca is either exclusively composed of large plates (i.e. *Ceratocystis* – although this genus is sometimes placed as the sister group of cornutes plus mitrates; Lefebvre and Vizcaino 1999), or consists of a frame of elongate marginal plates surrounding dorsal and ventral membranes of smaller tessellated plates (other cornutes). In some forms, serially repeated openings penetrate the dorsal surface; these are interpreted as respiratory structures (e.g. Lefebvre 2003) or gill slits (e.g. Jefferies 1986; Smith 2005). Mitrate stylophorans tend to have a more weakly asymmetrical theca composed of larger plates; plating is often strongly differentiated between the two thecal surfaces (dorsal–ventral orientation is contentious in mitrates). In both cornutes and mitrates, the appendage is similar in structure, consisting of a wide proximal part, a single median element (the stylocone) and a distal part that is composed of a single row of stout ossicles and two rows of small covering plates (David *et al.* 2000; Lefebvre 2003; Smith 2005). This appendage occurs at one margin of the theca (anterior–posterior orientation debated in stylophorans) and is interpreted as an ambulacrum for feeding (e.g. Ubaghs 1968a; David *et al.* 2000; Lefebvre 2003) or a muscular locomotory organ (e.g. Jefferies 1986; Smith 2005; Rahman *et al.* 2009). A specialized body opening is located at

the opposite end of the animal to the appendage, and is often enclosed by multiple tooth-like plates; this is seen as the anus (e.g. Lefebvre 2003) or the mouth (e.g. Smith 2005), depending on the interpretation of the appendage (Ruta 1999a).

Helicoplacoids have a spirally plated, spindle- to bulb-shaped theca constructed of multiple rows of polygonal interambulacral plates and three recumbent ambulacra (Fig. 3A). The ambulacra, which form part of the body wall, consist of paired floor plates (Fig. 3C), with alternating pits for the tube feet podia, and multiple sheets of cover plates. The mouth is thought to be located on the lateral margin of the theca where the three ambulacra converge, with the anus situated at the upper pole (Durham and Caster 1963; Paul and Smith 1984; Sprinkle and Wilbur 2005; Smith 2008).

Helicocystoids have a spindle-like, spirally-plated body, a cup of tessellated plates and a short polyplated stem (Fig. 3B). The large spiral region consists of rows of polygonal interambulacral plates (some of which are spine like) and five recumbent ambulacra; the ambulacra are composed of paired floor plates (Fig. 3D) and several series of cover plates, and lead to the mouth, which is situated on the upper pole and surrounded by a frame of oral plates. The anus is a conical structure located at mid-height on the lateral side of the body. The lower part of the spiral region transitions abruptly into the cup, which is composed of irregular circlets of large polygonal plates. The stem consists of unorganized small circular plates (Smith and Zamora 2013).

Edrioasteroids have a discoidal to globular theca and lack erect feeding appendages (Fig. 4A). They possess five ambulacra, which are composed of floor plates and cover plates, and are arranged around a central mouth in a 2–1–2 pattern (shared DE, unpaired A, shared BC

ambulacra; Figs. 1H, 4A). The anus is located on the upper surface between the C and D ambulacra. A border of plates surrounds the mouth and is constructed with modified uniserial floor plates (e.g. *Protorophus*), interradial oral plates (e.g. stromatocystitids, Fig. 4E) or both oral plates and double biserial floor plates (e.g. *Kailidiscus*, Fig. 1I, K) (Zamora and Smith 2010; Zhao *et al.* 2010; Kammer *et al.* 2013; Zamora *et al.* 2013b).

Eocrinoids have a sack-like theca, multiple erect feeding appendages (brachioles) and, usually, an aboral stalk or stem (Fig. 4B–D, F, G). The theca is composed of numerous polygonal plates, which are either irregularly arranged, or organized into discrete circlets or zones. In many cases, the theca is covered in sutural pores (epispires; Fig. 4F), which are thought to have been involved in respiration (Sprinkle 1973). The brachioles are long and slender, consisting of floor (brachiolar) plates and cover plates (Fig. 4G); they arise from five ambulacra (arranged in a 2–1–2 pattern) situated on the upper surface of the theca (Fig. 4D, F). Brachioles are exothecal structures, meaning that they lack a direct connection to the interior of the thecal cavity (David *et al.* 2000). The aboral appendage takes the form of an elongate hollow stalk with irregularly arranged plates (e.g. *Gogia*, Fig. 4D) or a stem with cylindrical columnals (e.g. *Ubaghsicystis*), sometimes with a distal attachment structure; it is absent or highly reduced in a handful of taxa (e.g. *Lichenoides*) (Ubaghs 1968b; Sprinkle 1973).

PREVIOUS PHYLOGENETIC SCENARIOS

Despite improved knowledge of the morphology of Cambrian echinoderms, there is currently no rigorous cladistic analysis that incorporates all or even most of the relevant fossil taxa. Nevertheless, a number of attempts have been made to reconstruct early echinoderm

phylogeny by using restricted subsets of taxa that that are thought to encompass Cambrian echinoderm disparity. Such work has the potential to provide a robust phylogenetic framework for elucidating the evolutionary emergence of echinoderms, so long as the methodology is appropriate, and a consensus now seems to be emerging (Fig. 5). We briefly review previous work on the relationships of Cambrian taxa below.

Historically, most studies of the phylogeny of Cambrian echinoderms involved placing fossils on a tree by hand. One such study was by Ubaghs (1971, 1975), who presented a phyletic diagram in which asymmetrical (i.e. cinctans, ctenocystoids, solutes and stylophorans) and spiral (i.e. helicoplacoids) forms evolved before pentaradial echinoderms, and therefore belong to the echinoderm stem group; however, the branching order of the different stem-group taxa was left ambiguous. This view was broadly accepted by many echinoderm workers at the time (e.g. Paul 1977; Philip 1979). A radical alternative scenario was proposed by Jefferies and co-workers, who argued that stylophorans and solutes are not echinoderms, but are instead basal chordates ("calcichordates"; e.g. Jefferies 1968, 1986, 1990; Jefferies *et al.* 1996). Under this model, stylophorans are depicted as stem- and crown-group chordates, with most solutes stem-group chordates – if correct, this would have major implications for the origins and early evolution of echinoderms and chordates, for instance implying that stereom is a deuterostome sympleisomorphy, rather than an echinoderm synapomorphy. The calcichordate model has been disputed in a number of papers (e.g. Philip 1979; Peterson 1995; Parsley 1997; Ruta 1999a; Lefebvre 2000); some of the strongest evidence against it comes from molecular biology, with comparisons of the genetic sequences of extant taxa showing that the key genes responsible for stereom formation in echinoderms are not found in chordates (Bottjer *et al.* 2006). This, coupled with substantial differences in the chemical composition of the skeleton in modern chordates (hydroxyapatite), echinoderms (calcite) and

hemichordates (aragonite), indicates that any fossils with a stereom skeleton (including solutes and stylophorans) should be interpreted as echinoderms. More recently, David and Mooi (1999) and David *et al.* (2000) presented a new phylogeny in which the various non-radial Cambrian taxa are derived, most closely related to crinoids (stylophorans) and eocrinoids (cinctans, ctenocystoids and solutes), with helicoplacoids and edrioasteroids at the base of the tree. In this phylogeny, stylophorans belong to the echinoderm crown group.

All of these studies are useful as they depict different hypothesis of how Cambrian groups are related to one another, but they are highly subjective because they superimposed character state changes onto a preferred evolutionary scenario (e.g. Ubaghs 1975; Jefferies 1986; David *et al.* 2000) or included characters that are based on very speculative interpretations of fossil morphology (e.g. Jefferies 1997). Formal, objective, cladistic analysis is essential to rigorously determine the evolutionary relationships of fossil taxa, but has only rarely been applied to Cambrian echinoderms. The first formal cladistic analyses of the relationships of early echinoderms were by Smith (1984) and Paul and Smith (1984), who recovered a tree with cinctans, ctenocystoids, helicoplacoids, solutes and stylophorans at the base, eocrinoids and rhombiferans allied with crinoids in a pelmatozoan clade and edrioasteroids in the eleutherozoan stem group. Sumrall (1997) conducted a cladistic analysis of a number of Palaeozoic taxa and obtained a rather different tree topology, with cinctans, ctenocystoids, solute and stylophorans forming a derived monophyletic group nested within the Blastozoa. The most recent cladistic analysis of Cambrian echinoderms was by Smith and Zamora (2013), who included nine fossils and 17 characters, obtaining a tree that shows the early evolution of the phylum through bilateral (ctenocystoids), asymmetrical (cinctans and solutes), triradial (helicoplacoids) and pentaradial (helicocystids, eocrinoids and

edrioasteroids) forms. This is the most up-to-date and robust phylogeny of Cambrian taxa currently available; it is used as the evolutionary framework in this paper (Fig. 5).

ROOTING THE ECHINODERM TREE

Some of the most significant differences between the phylogenies outlined above are the product of how the echinoderm tree is rooted. For example, David *et al.* (2000) used *Arkarua*, a tiny Ediacaran fossil that has been interpreted as an echinoderm (Gehling 1987; Mooi and David 1998), to root their tree. *Arkarua* is very poorly preserved and lacks distinctive morphological characters; it seems to exhibit pentaradial symmetry, but does not possess a mineralized skeleton. Moreover, the details of the ambulacra, if any, and the location of the main body openings are entirely unknown. Selecting *Arkarua* as the root for echinoderms has the effect of drawing pentaradial forms to the base of the tree, even though it is not possible to identify any other characters shared with these taxa. This is consistent with the known stratigraphic record of echinoderms, which shows that the oldest articulated specimens had a radial structure; the first echinoderms to appear in Laurentia were the triradial helicoplacoids, in Cambrian Stage 3, while in Gondwana the pentaradial eocrinoids appeared at approximately the same time (Smith *et al.* 2013; Zamora *et al.* 2013a). However, the early fossil record of echinoderms is strongly influenced by both taphonomic and sampling biases (Zamora *et al.* 2013a), and thus should not be read as a direct record of their evolutionary history. Furthermore, the appearance of very different fossil forms in Laurentia and Gondwana at about the same time is highly suggestive of a gap in the earliest record of the phylum (Zamora *et al.* 2013a). Coupled with uncertainties over the echinoderm affinities of *Arkarua* (Budd and Jensen 2000), this suggests that an alternative root is needed to resolve the phylogeny of early echinoderms.

Another possibility for rooting the echinoderm tree is suggested by the ontogeny and sister-group relationships of modern species. During their development, extant echinoderms pass through a bilateral larval stage and an asymmetrical metamorphosis, before the pentaradial adult emerges (Smith 2008). Moreover, extant hemichordates – the sister group of echinoderms – show near-perfect bilateral symmetry throughout their ontogeny, and this mode of symmetry is a deuterostome symplesiomorphy (Cameron 2005; Smith 2005). Taken together, this points towards bilateral symmetry being plesiomorphic for echinoderms, and strongly suggests that any forms with primary bilateral symmetry belong close to the base of the tree. The recently discovered Cambrian fossil *Ctenoimbricata* and the earliest ctenocystoids (*Courtessolea* and undescribed specimens from Morocco, Fig. 1B) exhibit a stereom skeleton and near-perfect bilateral symmetry (Domínguez Alonso 2004; Zamora *et al.* 2012; Smith *et al.* 2013), and so are excellent candidates for rooting the echinoderm tree. All of these forms have an anterior mouth and a posterior anus defining a clear anterior–posterior axis. In addition, they possess a complex feeding apparatus with a downward-facing mouth that is very different to the feeding structures (ambulacra) of derived echinoderms, and they are interpreted as pharyngeal basket feeders (Rahman and Clausen 2009; Zamora *et al.* 2012); this feeding mode is hypothesized to be ancestral to the deuterostomes (Cameron 2002, 2005; Gonzalez and Cameron 2009). These taxa provide a convincing root for all echinoderms (Fig. 5), and can be considered as good potential outgroups for future cladistic analyses of early echinoderms.

SPIRALLY-PLATED FOSSILS AND THE ORIGIN OF PENTARADIAL SYMMETRY

Although there are several bilateral, asymmetrical and pentaradial forms, only a single clade of Cambrian echinoderms shows triradial symmetry: the helicoplacoids (Fig. 3A). First described by Durham and Caster (1963), helicoplacoids are characterised by a spirally-plated body, three twisted ambulacra, an anus on the upper pole and a mouth in a lateral position. The phylogenetic position of this enigmatic extinct group is debated; they are either considered as stem-group echinoderms that originated prior to the emergence of pentaradial symmetry (e.g. Ubaghs 1975; Paul and Smith 1984; Smith 2008), or as a derived group of echinoderms that have secondarily lost pentaradial symmetry (e.g. Mooi and David 1998; Sprinkle and Wilbur 2005). Consequently, the group figures prominently in most scenarios for the evolution of pentaradial symmetry.

New spiral echinoderms from the Cambrian of Morocco (Smith and Zamora 2013) clarify the position of helicoplacoids and shed light on the evolution of pentaradial symmetry in early echinoderms. These fossils, the helicocystoids (Fig. 3B), consist of three main regions: (1) a spirally-plated body with five ambulacra arising from a mouth situated on the upper pole; (2) a basal cup constructed with tessellated plates; and (3) a polyplated distal stem. Helicocystoids show certain similarities to helicoplacoids, most notably the possession of a spiral body with ambulacra embedded in the body wall, but they differ in having the mouth in an apical position (as opposed to a lateral one). Moreover, helicocystoids display five ambulacra and an oral frame comparable to that of more derived pentaradial forms (Kammer *et al.* 2013; Smith and Zamora 2013), and their cup and stem are similar to those of some Cambrian stemmed echinoderms (e.g. *Gogia*). They differ from stemmed echinoderms,

however, in lacking erect feeding appendages; the ambulacra of helicocystoids are recumbent and more alike those of some edrioasteroids. Based on this mixture of characters, helicocystoids are interpreted as being close to the latest common ancestor of crown-group echinoderms (Fig. 5). The shift in the position of the mouth from lateral in helicoplacoids to terminal in helicocystoids (a synapomorphy of all pentaradial echinoderms) indicates that torsion, a key phase in echinoderm development where the mouth is brought into an apical position for feeding, evolved progressively (Smith and Zamora 2013), perhaps associated with the adoption of obligate larval attachment at the anterior (Smith 2008). Helicocystoids fill the gap between helicoplacoids and crown-group echinoderms, finally revealing how a pentaradial structure originated in echinoderms.

DIVERSIFICATION OF PENTARADIAL FORMS

All extant echinoderms are pentaradial, and such forms also dominated during much of the Palaeozoic (Sumrall and Wray 2007). Traditionally, two major groups of pentaradial echinoderms are recognized, pelmatozoans (e.g. crinoids) and eleutherozoans (e.g. asteroids, echinoids, holothurians and ophiuroids). Since 1973, when Sprinkle published his seminal work on blastozoan echinoderms, stemmed echinoderms or pelmatozoans have been classified in two major groups: crinozoans, the unique living representatives of which are crinoids, and blastozoans, which include a large number of extinct clades and grades (e.g. blastoids, eocrinoids and rhombiferans). Both groups are said to exhibit primary pentaradial symmetry, which is sometimes secondarily modified (Sumrall and Wray 2007), but they are supposedly differentiated by the construction of their feeding appendages (Sprinkle 1973; David *et al.* 2000). In crinozoans, these are termed arms, and they are composed of plates that contribute to the theca (brachials), as well as ambulacral flooring and cover plates (note that

the floor plates are uncalcified in most fossil crinoids; Guensburg and Sprinkle 2009). Based on the anatomy of modern crinoids, arms are inferred to have housed coelomic extensions of the main body cavity. In contrast, blastozoans are thought to be characterised by the possession of brachioles, which are relatively simple structures mounted on floor plates, without a direct connection to the main body cavity. However, recent discoveries of arm-like appendages in the Cambrian forerunners of rhombiferans (Fig. 4H), in addition to observations of solutes and diploporans (e.g. *Eumorphocystis*), have cast doubt on this division, strongly suggesting that arms are not unique to crinoids (Zamora and Smith 2012). Contrary to previous suggestions, it seems that the construction of pelmatozoan feeding appendages was actually quite variable during the Cambrian, and this character should hence not be used as the sole basis for differentiating major groups of pentaradial echinoderms.

Another group of typical pentaradial fossil echinoderms are the edrioasteroids. They vary in the construction of their ambulacra; derived edrioasteroids have either uniserial (isorophids) or biserial (edrioasterids) floor plates, while Cambrian forms are more diverse with uniserial (e.g. *Protorophus*), biserial (e.g. *Cambraster*) or quadriserial (e.g. *Kailidiscus*) floor plates (Zhao *et al.* 2010; Zamora and Smith 2012; Zamora *et al.* 2013b). It is only recently, following the discovery of lower Palaeozoic fossils with well-preserved internal details, that the homology of these different sets of floor plates has been clarified (Sumrall and Zamora, 2011; Zamora 2013). This showed that the quadriserial ambulacra of *Kailidiscus* are composed of outer and inner series of floor plates, with the outer (abradial) set topologically and structurally similar to the biserial floor plates of edrioasterids, *Cambraster* and *Stomatocystites* (indicating homology). Sumrall and Zamora (2011) argued that these plates are also homologous with the hood plates in pyrgocystids. The inner floor plates of *Kailidiscus* have been interpreted as homologues of the floor plates of isorophids, which,

with the exception of pyrgocystids, lack the outer floor plates. This new data, together with the results of a cladistic analysis (Zamora 2013) and detailed study of oral plating (Kammer *et al.* 2013), suggests that edrioasteroids represent a paraphyletic grade of early echinoderms.

One of the chief problems for understanding the diversification and relationships of pentaradial echinoderms is that it is difficult to identify homologies between the various extinct groups because of their disparate morphologies (Sumrall and Wray 2007). Some workers have attempted to use the extraxial–axial theory (EAT), a model of body wall homologies that assumes all echinoderms possess a skeleton that can be divided into axial (associated with the water vascular system) and extraxial (associated with the rest of the body wall) regions, to infer homologies among fossil taxa (e.g. Mooi and David 1998; David and Mooi 1999; David *et al.* 2000). However, because the EAT relies on regional homologies that do not vary greatly across echinoderms, it does not yield sufficient characters for determining the phylogeny of early echinoderms (Sumrall and Waters 2012). An alternative model, universal elemental homology (UEH), works by identifying homologous plates between taxa, and hence is more useful for resolving the relationships of pentaradial echinoderms (Sumrall 2008, 2010; Sumrall and Waters 2012). It was originally developed for the study of relatively derived blastozoans, such as coronoids, blastoids, hemicosmitoids and glyptocystitoid rhombiferans; more recently, it has been extended to additional fossil groups, including Cambrian representatives of the classic blastozoan groups (e.g. eocrinoids), crinoids and edrioasteroids (Kammer *et al.* 2013). A formal cladistic analysis based on UEH and including a wide range of Cambrian echinoderms is still awaiting publication, but the preliminary study of Kammer *et al.* (2013) has already yielded some interesting results. Based on the morphology and structure of the plates associated with the peristome (Fig. 6), it seems that some edrioasteroids (e.g. isorophids) are more closely related to early blastozoans (e.g. gogiid

eocrinoids), while other edrioasteroids (e.g. *Cambraster*) are closer to derived blastozoans (e.g. glyptocystitoids) and crinoids. Thus, UEH shows that several groups previously thought to be quite distant from one another are actually close relatives, meaning that several classes (e.g. eocrinoids and edrioasteroids) are paraphyletic or polyphyletic. This radically alters the traditional view of the diversification of pentaradial echinoderms (e.g. Sprinkle 1973) and raises new questions that will need to be addressed in the future.

OPEN QUESTIONS

Despite major recent advances in our understanding of the morphology and evolution of early echinoderms, there are still a number of uncertainties concerning their earliest history. One key issue relates to the known spatial distribution of Cambrian fossils; while we now have a relatively good picture of echinoderms from the Cambrian of Laurentia and many parts of Gondwana (Smith *et al.* 2013; Zamora *et al.* 2013a), the record from other palaeogeographical areas is still very patchy. This is significant because palaeobiogeography probably played a key role in controlling the evolution of Cambrian taxa; some of the oldest representatives of the main groups appear earlier in Gondwana than in Laurentia, and this is most likely linked to differences in their ecology during the Cambrian (Zamora 2010). Further study of under-represented areas, such as Baltica and Siberia, should help build up a more complete global record of Cambrian echinoderms, shedding additional light on their origin and initial radiation.

Determining homologies between different groups remains a major challenge for reconstructing the phylogeny of early echinoderms. While a number of rigorous phylogenetic analyses have been conducted for single groups (e.g. Lefebvre and Vizcaino 1999; Ruta

1999b; Sumrall and Brett 2002; Parsley and Sumrall 2007; Smith and Zamora 2009; Parsley *et al.* 2012; Zamora 2013; Zamora *et al.* 2013c), there are very few robust phylogenies incorporating multiple groups, in part due to the problem of linking disparate forms with unambiguous statements of homology (Smith and Zamora 2013). Recent discoveries from the Cambrian have helped clarify the relationships among some groups; for example, *Ctenoimbricata* allows us to identify homologies between ctenocystoids and cinctans (Zamora *et al.* 2012), while *Helicocystis* shares characters with eocrinoids and helicoplacoids (Smith and Zamora 2013). Nevertheless, we are still unable to confidently determine homologies among many other major clades, particular between radial and pre-radial forms. Addressing this problem will require not only the discovery of new 'transitional' species, but also the detailed description of fossilized ontogenies (Sumrall and Wray 2007), which could help us better understand the development of extinct taxa and hence the morphological transformations that occurred during their evolution.

Better progress is being made in terms of understanding the relationships of pentaradial fossil echinoderms, and a formal phylogenetic analysis that includes all such forms is close to completion (Kammer *et al.* 2013), informed by homology statements based on the conserved oral regions of the skeleton (Sumrall and Waters 2012). Unfortunately, the oral areas of Cambrian echinoderms are often incompletely known and/or poorly understood, and hence future efforts should focus on the recognition and description of these important anatomical parts.

Echinoderms possess an extensive fossil record, and the development and relationships of modern species are well characterised. For many years, our understanding of the origin and earliest evolution of the phylum has remained incomplete; however, based on new fossils

from the Cambrian and the application of novel techniques/approaches, a more complete picture of the emergence of echinoderms is now beginning to emerge. Some important gaps in our knowledge still need to be filled, but we are close to achieving a consensus on the phylogeny and evolution of echinoderms. This will help us decode the pattern and process of assembly of the echinoderm body plan.

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FIGURE CAPTIONS

FIG. 1. Characters of extant and extinct echinoderms. A. Modern asteroid exhibiting pentaradial symmetry. B. Cambrian ctenocystoid showing bilateral symmetry. Specimen number NHMUK EE 15428. C. Cambrian solute showing asymmetry. Specimen number NHMUK EE 4971. D, E. Stereom microstructure in a Cambrian stylophoran (modified from Clausen and Smith 2005, fig. 3). F, G. Isolated plate and detail of stereom microstructure in a

modern echinoderm (courtesy of Przemyslaw Gorzelak). H–J. Ambulacral construction in the Cambrian edrioasteroid *Kailidiscus* (courtesy of Colin Sumrall). H. General view of the oral area with cover plates arranged in a 2–1–2 pattern. I. External view of an ambulacrum showing the food groove. Note that the cover plates are not present, so the podial pores are visible. J. External view of an ambulacrum showing the exposed parts of the floor plates and multiple sets of cover plates. K. Internal view of an ambulacrum showing four series of floor plates and the podial pores. Abbreviations: adfp, adradial floor plates; abdf, abradial floor plates; cp, cover plates; pp, podial pores. Specimens A, C are original specimens; B and H–J are latex casts whitened with NH_4Cl sublimate and specimens D-G are SEM photographs.

FIG. 2. Cambrian asymmetrical echinoderms. A–C. The cinctan *Gyrocystis testudiformis*. A. Dorsal view of a complete specimen. MPZ2009/150. B. Ventral view of a partial specimen without the posterior appendage MPZ2009/155. C. Frontal view showing the main body openings. MPZ2008/4. D. The solute *Castericystis vali*. NHMUK EE 44. E. The stylophoran *Ceratocystis perneri*. (Courtesy of Bertrand Lefebvre, figured in Zamora et al. 2013a) . F–H. The ctenocystoid *Ctenocystis utahensis*. F. Dorsal view. USNM 163252. G. Frontal view. H. Lateral view. USNM 595079. Abbreviations: an. Anus, aa. Anterior appendage, ap. Appendage, ct. Ctenidium, fg. Food groove, mr. Marginal ring, op. Operculum, pa. Posterior appendage, pe. Peristome, so. Suroral plate, th. Theca, vi. Ventral integument. Specimens A–C and E–H are from latex casts whitened with NH_4Cl sublimated. Photograph D is from an original specimen.

FIG. 3. Cambrian spiral echinoderms. A, C. The helicoplacoid *Helicoplacus gilberti* A. General view of the theca, with a lateral mouth and three ambulacra. Specimen UT TMM 2041TX1a. (Courtesy of Bryan Wilbur). C. View from the interior of the ambulacral flooring

plates NHM UK 5343. B, D. The helicocystoid *Helicocystis moroccoensis*. B. General view of the theca, with a terminal mouth and five ambulacra NHM UK EE15375. D. View from the exterior of food groove associated with floor plates NHM UK EE15373. Floor plates are indicated in green. All specimens are from latex casts whitened with NH_4Cl sublimated.

FIG. 4. Cambrian pentaradial echinoderms. A. The edrioasteroid *Cambraster cannati*. MPZ2009/1232. B, C. The imbricate eocrinoid *Kinzercystis durhami* showing general body structure (B) and pentaradial oral area with brachioles (C). MCZ 114807. D. Gogiid eocrinoid showing general structure of the body. USNM 553409. E. Ambulacral structure of the edrioasteroid *Cambraster tastudorum* showing how the floor plates continue with the oral plates (interradial mouth plates). NMVP107060. F. D. Detail of the oral area in *Kinzercystis durhami* showing how simple feeding appendages (brachioles) alternate in each ambulacra. MCZ 114808. G. Detail of brachioles. H. Complex arm of *Dibrachicystis purujoensis* MPZ2009/1236. Abbreviations: A–E. Ambulacra, br. Brachials, brs. Brachioles, cp. Cover plates, fp. Floor plates, pe. Peristome, pp. Podial pores, st. Stem, th. Theca. All specimens are latex casts whitened with NH_4Cl sublimate.

FIG. 5. Phylogeny of select Cambrian echinoderms (after Smith and Zamora 2013).

FIG. 6. Oral region homologies in pentaradial echinoderms based on universal elemental homology (after Kammer *et al.* 2013). A. The plesiomorphic cladid crinoid *Carabocrinus treadwelli*. OU 9127. B. The glyptocystitoid rhombiferan *Quadrocystis graffhami*. OU 8972. C. The edrioasteroid *Kailidiscus chinensis*. GM 2103. D. The gogiid eocrinoid *Sinoeocrinus lui*. GTBM95265. E. The imbricate eocrinoid *Lepidocystis* cf. *L. wanneri*. MCZ 628. F. The edrioasteroid *Anedriophus moroccoensis*. FSTG/AABCBb-OI-25. Red: oral plates that form

the border of the peristome. Green: ambulacral flooring plates. Yellow: ambulacral cover plates. Blue: primary peristomial cover plates. Pink: oral frame plates. Photographs A, B are from original specimens, and C-F are from latex casts whitened with NH_4Cl sublimated.

SUPPLEMENTARY DATA 1. Interactive pdf with a 3D reconstruction of *Ctenoimbricata spinosa*, from the middle Cambrian of Spain.

REPOSITORY

All figured specimens are deposited in the following public institutions and are available for researchers.

FSTG: Faculté des Sciences et Techniques Guéliz, Université Cadi Ayyad. Marrakech, Morocco.

GM and GTB: Paleontology Museum of Guizhou University, China

MCZ: Museum of Comparative Zoology, Harvard University, USA.

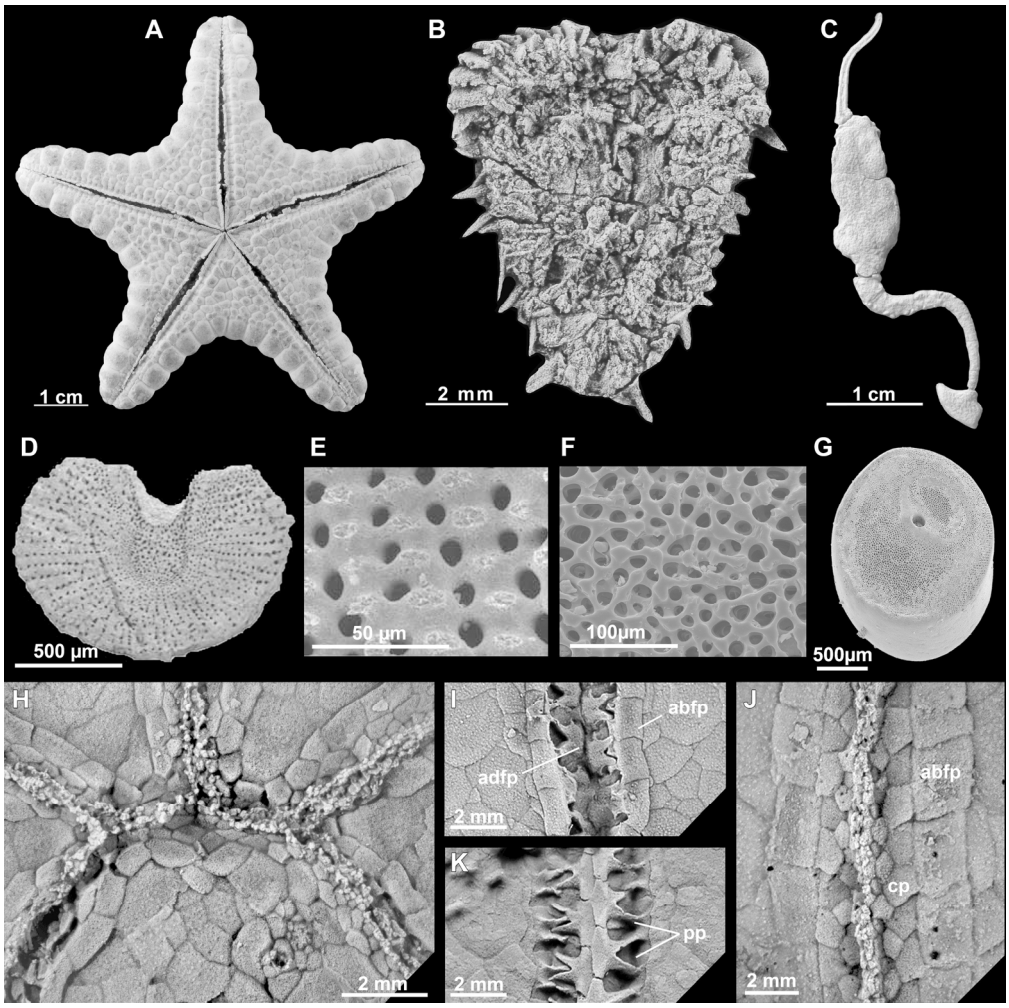
MPZ: Museo Paleontológico de la Universidad de Zaragoza, Spain.

NHM: Natural History Museum, London.

OU: Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, USA.

USNM: U.S. National Museum of Natural History, Washington DC, USA.

UT TMM: Texas Memorial Museum, USA.



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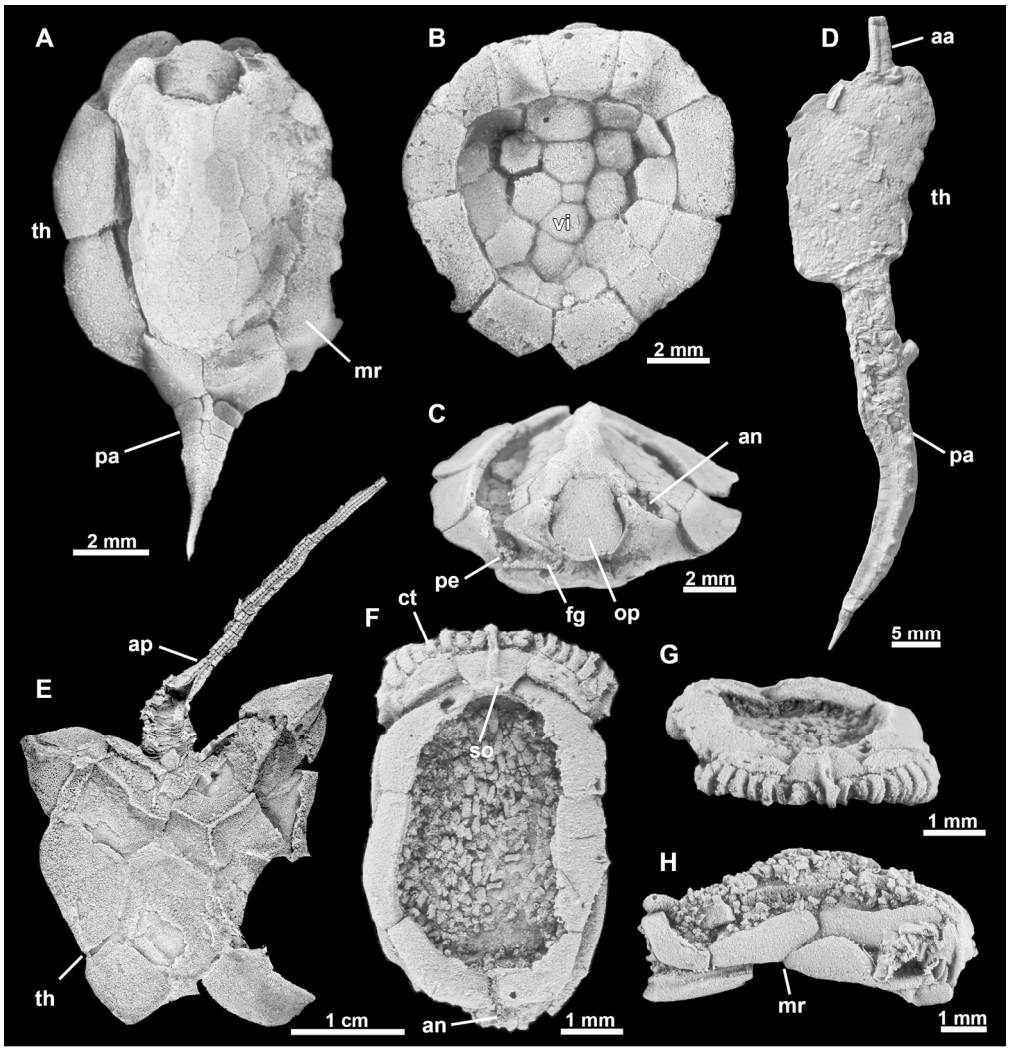

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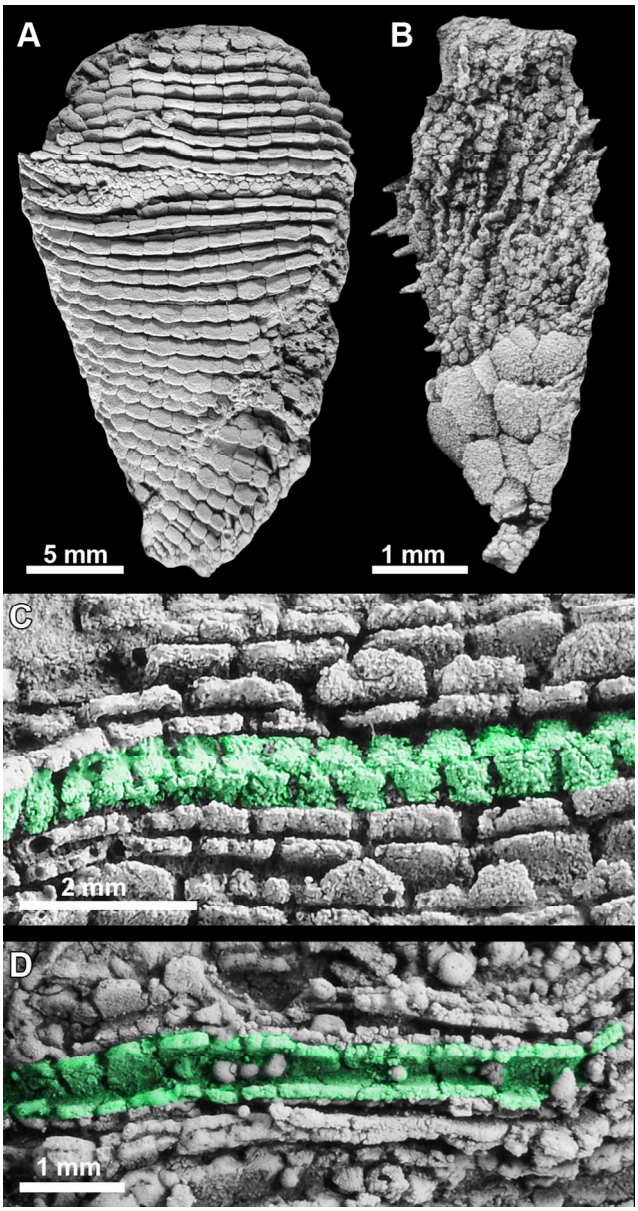

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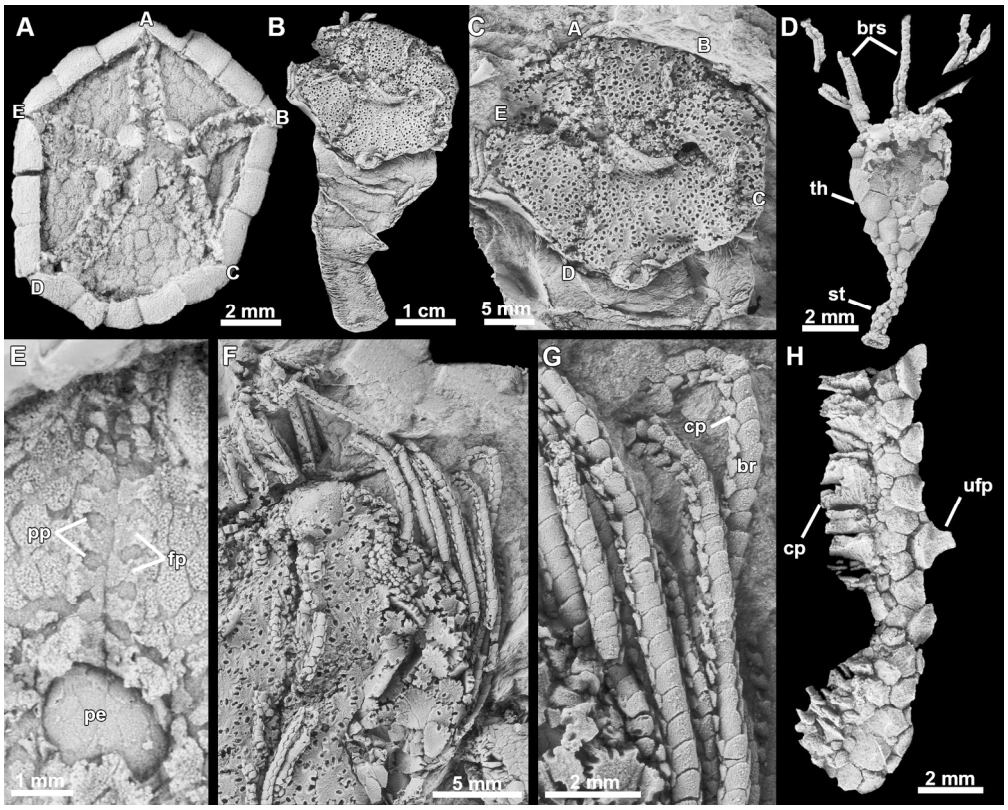

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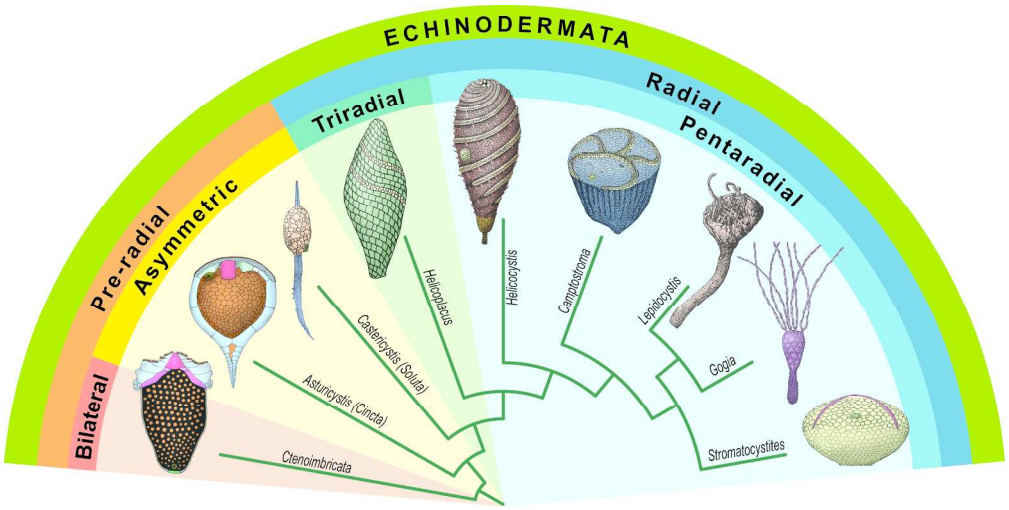

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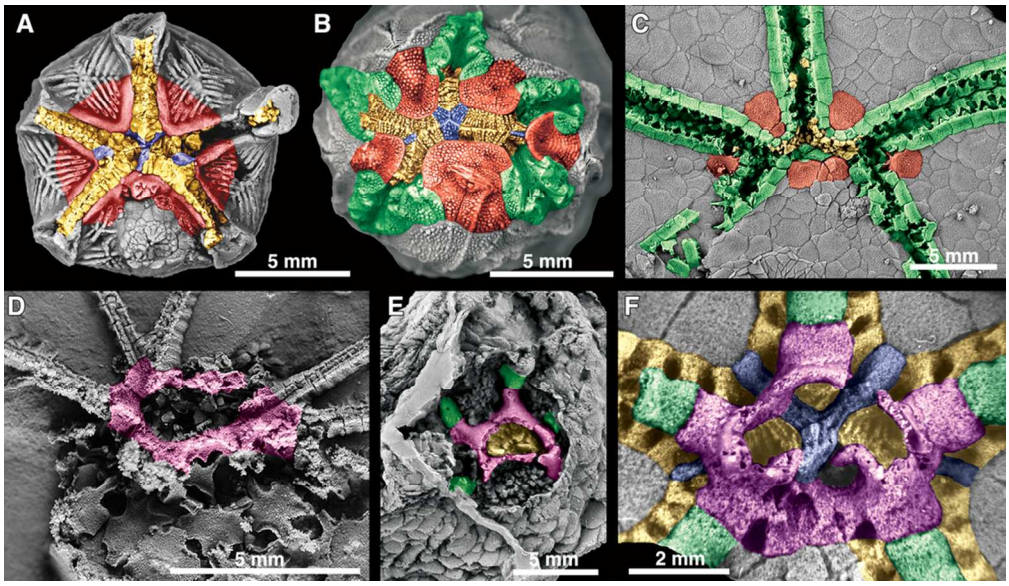

95x54mm (300 x 300 DPI)

Ctenoimbricata spinosa

Samuel Zamora, Imran A. Rahman and Andrew B. Smith, 2012

Ctenoimbricata spinosa (Click to launch; Adobe Reader 7.0 or later)

Ctenoimbricata spinosa gen. et sp. nov. Cambrian Series 3, Stage 5, Purujosa, Spain. X-ray micro-tomography undertaken on a Metris X-Tek HMX-ST at the Natural History Museum, London. Reconstructed as a virtual fossil using the SPIERS software suite.